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CLIMATE-GROWTH RELATIONSHIPS OF NORWAY SPRUCE BEYOND ITS NATURAL DISTRIBUTION RANGE

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ABSTRACT

The influence of human activities on climate system is nowadays clear and over the years it is growing and strengthening. In many regions of the world, changing patterns in climate events are leading to major changes in hydrological and biological systems, causing strong impacts on natural systems with the shift of geographic ranges, seasonal activities, migration patterns, abundances and interactions in many species and, subsequently, increasingly affecting also human civilization and activities. Therefore, it is clear that tree species will shift their distribution range to track climate change moving northward. On the other hand, further south, there is a greater potential for loss of actual species and the possibility of immigration for warmth-requiring ones. However, the current pace of climate change is much faster than any other change occurred in the past and this it is threatening especially plant species, given their intrinsic slow speed of movement: taxa that fail to cope fast enough with these rapidly changing climate regimes will face extinction.

The aim of this thesis is to study, using dendrochronological techniques, the growth response to climate of Norway spruce (*Picea abies*) beyond its natural distribution. The work has been conducted in Iceland, to see how the species is behaving beyond its current northern natural range; moreover, further Norway spruce samples have been collected in two plantations in Marche and Emilia Romagna Regions, Central Italy, to study species' growth trends in correspondence of the southern distribution limit and beyond it. In order to better understand growth dynamics within the Icelandic sites, we also collected more samples from two other tree species, *Picea sitchensis* (Sitka spruce) and *Pinus contorta* (lodgepole pine).

The analysis of the radial increment of the trees showed an overall high fluctuation in the tree ring width, beginning in the 1990s both in Italian and Icelandic sites. This pattern is maybe related to climate, testifying an increase of hot and dry summers in the last thirty years. Moreover, the climategrowth correlation profiles highlighted a diverse action of climate on tree growth, which seems to vary according to latitude: at northern latitudes, within the Icelandic sites, Norway spruce growth is mainly affected by temperatures, especially mean summer temperature (June July and August), whereas, towards southern latitudes, within the Italian sites, precipitation regime plays a major role on the species' growth, especially during July of the current year and June of the previous year. The Emilia Romagna site showed an overall low correlation with climate, probably due to the shortness of available data. Sitka spruce and lodgepole pine climate-growth relationships proved useful to better understand growth patterns in Iceland, supporting the growth trend showed by Norway spruce.

Considering the present warming climate scenario and the general uncertainties on tree migration and growth patterns, these results can contribute for a better understanding on the growth of the species outside its distribution and therefore on how spruce might behave in the future. Moreover, these results can be useful in further developing strategies such as *assisted migration*: knowing the future trees requirements can facilitate the movement of species to improve natural population dynamics and range expansion in a climate change scenario.

RIASSUNTO

L'influenza delle attività umane sul clima è sempre più evidente e negli anni sta crescendo e intensificandosi. In molte regioni del mondo, i cambiamenti climatici stanno ampiamente modificando i sistemi idrologici e la biosfera, causando forti impatti sui sistemi naturali e sulle specie, i cui areali di distribuzione, fenologia, pattern migratori, abbondanza e interazioni si stanno rapidamente alterando, arrivando ad avere ripercussioni anche sulle attività umane. Come conseguenza, è oramai chiaro che gli alberi modificheranno la loro distribuzione migrando verso nord, seguendo i cambiamenti climatici. Verso sud, invece, vi sarà una maggiore probabilità di perdita di specie e di immigrazione di organismi adattati a climi via via più caldi. Tuttavia, l'attuale ritmo a cui il clima sta cambiando è molto più rapido di qualsiasi altro cambiamento avvenuto in passato e ciò minaccia soprattutto le specie vegetali, in quanto organismi per lo più sessili: i taxa che non riusciranno a adattarsi abbastanza velocemente a questi regimi climatici in rapida evoluzione andranno incontro all'estinzione.

Lo scopo di questa tesi è studiare, utilizzando tecniche dendrocronologiche, le relazioni tra clima e accrescimento nell'abete rosso (*Picea abies*) oltre i limiti della sua distribuzione naturale. Lo studio è stato condotto in Islanda, al fine di osservare il comportamento della specie introdotta oltre il limite settentrionale della distribuzione. In aggiunta, altri campioni di abete rosso sono stati prelevati in due piantagioni nelle Regioni Marche e Emilia-Romagna, per studiare le risposte in corrispondenza e oltre il limite meridionale della distribuzione della specie. Per comprendere al meglio le dinamiche di crescita all'interno dei siti islandesi, abbiamo inoltre raccolto campioni anche di *Picea sitchensis* e *Pinus contorta*.

L'analisi degli incrementi radiali ha mostrato un'elevata variabilità dell'ampiezza anulare a partire dagli anni '90, sia nei siti italiani sia in quelli islandesi. Tale andamento è probabilmente legato al clima, a testimonianza di un aumento delle estati calde e secche negli ultimi trent'anni. Inoltre, i profili di correlazione hanno evidenziato una diversa azione del clima sull'accrescimento. Le risposte, infatti, sembrano variare a seconda della latitudine: nei siti islandesi, la crescita dell'abete rosso è influenzata principalmente dalle temperature, in particolare dalle temperature estive (giugno luglio e agosto); verso le latitudini meridionali, è invece il regime delle precipitazioni ad avere un ruolo dominante, soprattutto nei mesi di luglio dell'anno in corso e giugno dell'anno precedente. Tra i siti italiani, il sito emiliano ha mostrato una correlazione con le variabili climatiche complessivamente inferiore, probabilmente a causa della ridotta disponibilità dei dati. Le relazioni tra clima e accrescimento di *Picea sitchensis* e del *Pinus contorta* si sono rivelate utili per comprendere meglio i pattern di crescita in Islanda, confermando i trend mostrati dall'abete rosso.

Considerando l'attuale scenario climatico e le incertezze generali sulle modalità di migrazione degli alberi e, di conseguenza, sui relativi trend di crescita, i risultati di questa tesi possono ampliare le conoscenze sul comportamento delle specie al di fuori della loro areale di distribuzione e quindi su come le diverse specie arboree potrebbero comportarsi in futuro. Inoltre, tali risultati possono essere utili per sviluppare strategie quali la *migrazione assistita*: conoscere le esigenze delle diverse specie in un futuro

prossimo potrà agevolare le dinamiche naturali delle popolazioni e favorire operazioni di espansione degli areali in uno scenario climatico in evoluzione.

1. INTRODUCTION

As reported by the IPCC (2014) in the Fifth Assessment on Climate Change, the influence of human activities on climate system is clear and over the years it is growing and strengthening. The strongest impacts of climate change involve natural systems (IPCC 2014). In fact, in many regions of the world, changing patterns in climate events (e.g. intensification of extreme meteorological events) are leading to major changes in hydrological and biological systems, with the shift of geographic ranges, seasonal activities, migration patterns, abundances and interactions in many species (IPCC 2014). Subsequently, these changes are increasingly affecting also human civilization and activities, such as farming (IPCC 2014). Projections made in the last years suggest that by 2100 temperatures will increase between about 2-3 °C (Ireland and the UK, Central Europe) and 4–5 °C (northern Boreal and parts of the Mediterranean regions) and atmospheric CO₂ concentration will increase to at least 486 ppm (in some scenarios even beyond 1000 ppm) compared to the pre-industrial concentration of 280 ppm (Lindner et al. 2010). In the best-case scenario (RCP2.6, stringent mitigation scenario), according to the projections made by the IPCC (2014) among the Representative Concentration Pathways, the increase of global mean surface temperature by the end of the 21st century (2081–2100) relative to 1986–2005 is likely to reach values from 0.3°C to 1.7°C.

The largest temperature increases will be at higher latitudes in the Northern Hemisphere, with winter warming that could increase by 40% above global mean temperature in 2100 (Kaplan and New 2006; MacDonald, Kremenetski, and Beilman 2008; Soja et al. 2007). This area is currently covered by ice sheets and biomes such as tundra and taiga and could experience major changes in species and habitat distribution over the next years, arriving to influence high-latitude albedo and provide a positive feedback, further enhancing global warming (MacDonald, Kremenetski, and Beilman 2008).

Such huge climate system modifications are expected to cause significant changes in ecosystem structure (e.g., predominant vegetation, age class, distribution, and species composition), function (e.g productivity, decomposition, nutrient cycling, and water flows), and distribution within and across landscapes (Leech, Almuedo, and Neill 2011). This, in addition to the rapid rates projected for near future, pose a fundamental challenge: Taxa that fail to cope fast enough with these rapidly changing climate regimes will face extinction (Davis and Shaw 2001; Gritti, Smith, and Sykes 2006).

1.1. Effects of climate change on forest species distribution

Over the centuries species and ecosystems have changed their distribution in order to keep pace with climate variation, with the best example represented by the shifts of tree distributions during the climatic warming after the recent glacial retreat (Malcolm et al. 2002; Leech, Almuedo, and Neill 2011). However, tree migration potential and patterns are still not fully understood and the rate at which they are migrating (especially long distance dispersal) under the ongoing climate changes is still poor investigated (Malcolm et al. 2002; Leech, Almuedo, and Neill 2011). What is clear is that the pace of actual climate changes is much faster the any other change that has occurred in the past (Malcolm et al. 2002; Leech, Almuedo, and Neill 2011). This can be relevant especially for plants, and even more for trees, which naturally can migrate only at a much slower speed (Taggart and Cross 2009; Leech, Almuedo, and Neill 2011). As Aitken et al. (2008) suggests, trees will need to move more than 1000 m per year to keep up with the climate to which they are optimally adapted as it spreads poleward and up in elevation. On the other hand, a study of five tree species in the eastern United States shows very low probabilities of natural dispersal beyond 10-20 km from current species boundaries by 2100 (an average of 100-200 m per year) (Iverson, Schwartz, and Prasad 2004).

Nowadays it is clear that tree species will shift their distribution range to track climate change moving northward (Taggart and Cross 2009), with juveniles concentrated in cold climates, warm enough for contemporary colonization that were not previously suitable when mature individuals became established (Zhu et al. 2014). On the other hand, further south there is a greater potential for loss of actual species and the possibility of immigration for warmth-requiring species.(Sykes and Prentice 1995). This mechanism is valid also for the altitudinal gradient: with warmer climate, plants (and many other species) are moving upward, to colonize areas on average colder than those they previously inhabited (Dainese et al. 2017). However, another hypothesis, called *turnover hypothesis*, must also be considered: increasing temperature and precipitation could increase turnover rates (rapid growth, increased mortality, and elevated recruitment), hence with the juveniles concentrated in warmer climates, not in the cold (Zhu et al. 2014).

In this context of migrating species, more attention should be given to invasive species and which species should be defined as such. In fact, while affecting the distribution, spread, abundance, and impact of invasive species (Gritti, Smith, and Sykes 2006), climate change will also challenge the definition of invasive species itself: some taxa that were previously invasive may diminish in impact, while other previously noninvasive species may become invasive (Hellmann et al. 2008). These are all reasons to carefully specify what is meant by an invasive species, term that should focus on species which have been recently introduced in a specific region and exert substantial negative impact on native biota, economic values, or human health (Lodge et al. 2006; Hellmann et al. 2008). Therefore, as Hellmann et al. (2008) suggest, native species that has expanded or modified their geographic distributions, moving into areas where they were previously absent, should not be considered invasive, unless they can causes discernable damage.

1.2. Assisted migration

In this scenario, new strategies have been developed to help threatened species to adapt and to avoid extinction. Perhaps the most important example is the so-called *assisted migration*. It is defined as "the purposeful movement of species to facilitate or mimic natural population or range expansion to help ensure forest plantations remain resilient in future climates" (Leech, Almuedo, and Neill 2011). It represents an important tool for helping plant and animal populations, communities, and ecosystems to respond and adapt to predicted ecosystem shifts within a changing climate (Leech, Almuedo, and Neill

2011). Assisted migration may be especially important for species and ecosystems with restricted ranges or physical barriers (e.g. oceans, habitat fragmentation), therefore unable to migrate to new habitat as it becomes available (Leech, Almuedo, and Neill 2011).

Over time this new concept has opened many debates about whether or not it should be used as tool to help species withstand climate change. In fact, many conservation biologists and ecologists consider moving species outside their current distribution to be too risky, the most problematic of it is the potential invasiveness of a species once introduced in a new area (Vitt et al. 2010). However, some biologists are now highlighting the importance of re-visiting the prohibition of species movement in order to prevent climate-driven extinction (Leech, Almuedo, and Neill 2011). In fact, as Vitt et al. (2010) suggests, well-planned translocations of species may reduce the risk of extinction, as well as increase the number of potential taxa creating new assemblages in a fluid landscape responding to the major climate changes we are experiencing.

1.3. *Objectives*

The aim of this thesis is to study, using dendrochronological techniques, the growth responses to climate of *Picea abies* beyond its natural distribution. The work has been conducted in Iceland, a place notoriously poor of trees, to see how introduced conifers are behaving beyond the northern limit of their natural range, especially in an almost pristine land. Moreover, other *Picea abies* samples have been collected in two plantations in Marche and Emilia Romagna Regions, Central Italy, to study species' growth trends in correspondence of the southern distribution limit and beyond.

In Iceland, the field work was carried out in multiple sites across the island with the help and supervision of the Icelandic Forest Service (Skógræktin), especially from Doctor Ólafur Eggertsson. The analysis has been conducted at the laboratories of the Icelandic Forest service situated in Mógilsá, north of Reykjavík. The Italian samples have been collected in Marche and Emilia Romagna Regions, while lab analysis has been conducted at the tree-ring lab of the TeSAF Dept. in Legnaro (PD), Italy.

This study can provide useful insights to understand and investigate concepts such as assisted migration and can describe the ability and the struggles of Norway spruce, to adapt and modify its distribution in a context of warming climate.

1.4. Iceland: particularities and relevance

Iceland is a volcanic island located in the North Atlantic, close to the Arctic Circle, within 63°23' N and 66°32' N latitude, about 290 km away from Greenland (Einarsson 1984). Given its latitude, the mean temperature of warmest month (July) of around 10° C (Einarsson 1984), and its vegetation cover, mostly formed by grasslands and tundra, it is considered to belong to the Sub-Arctic region, with a subpolar climate (Cfc, Köppen) (Arnfield 2020). The northernmost part of the country and the highlands are comprised in the Arctic region (mean temperature of the warmest month less than 10° C), with a tundra climate (ET, Köppen) (Einarsson 1984; Arnfield 2020; Arctic Centre, University of Lapland).

However, due to the Gulf Stream temperatures are mild and not extreme as other areas located at the same latitude.

Despite being considered as one of the countries with lowest percentage of forest cover in the world, Iceland has not always been so tree-poor over time. As reported by Eysteinsson (2017), fossil evidence indicates the presence of forest coverage on the island during the mid to late Tertiary (5-15 million years ago), with tree genera belonging to warm-temperate climates, like Sequoia, Magnolia, Sassafras, Pterocarya and beech (*Fagus* sp.). With succeeding glaciations, the Icelandic flora became less diverse, with pines and alders recognized to be the last species to disappear (Eysteinsson 2017). The only tree species able to come back in the present interglacial period (Holocene) are downy birch (*Betula pubescens* Erh.); rowan (*Sorbus aucuparia* L.), aspen (*Populus tremula* L.) and the tea-leaved willow (*Salix phylicifolia* L.) (Eysteinsson 2017; Blondal 1987).

As reported by Blondal (1987), around 1100 years ago at the time of the first settlement, birch forests and woodlands covered 25-30% of Iceland. Over time, the original forest cover has diminished by 95%, especially at the expense of birch stands (Eysteinsson 2017), due to the settlers need for fuel, charcoal, fodder, and grazing land (Blondal 1987). As stated by Eysteinsson (2017). the extent of birchwoods in Iceland probably reached a minimum of less than 1% of total land area around the mid-20th century, perhaps even less than 0.5%. Since then, an effort has been made to increase the forest cover through afforestation, reforestation and protection of relic woodland from grazing (Eysteinsson 2017; Blondal 1987).

Nowadays, alongside native forest protection, many exotic species have been tested and afterward established into the country in order to stop soil erosion, protect nature and enhance biodiversity, promote carbon sequestration and create an internal market for wood products (Snorrason and Kjartansson 2017). Aside birch forest, which added up to 43% of total forested area in 2010, the main exotic tree species are Siberian larch (*Larix sibirica*), Sitka spruce (*Picea sitchensis*), lodgepole pine (*Pinus contorta*), Norway Spruce (*Picea abies*) and black cottonwood (*Populus trichocarpa*). (Snorrason and Kjartansson 2017; Eysteinsson 2017). These species have been selected after many trials, which involved nearly 100 candidate species and various sources of seed around the world (Blondal 1987). After decades of intense afforestation efforts, today forests and other woodland cover 0.4% and 1.4%, respectively, of Iceland's area (figure 1).

As previously reported, Arctic regions are warming much faster than the global mean. This trend has been detected also for Iceland (Björnsson 2009). In particular, the temperature increase compared to the last century amounted to just over 0.7° C and it is projected to increase by 1° C compared to the current average temperature by 2050, even by 1.4-2.4° C by the end of the century (Björnsson 2009). Environmental effects are evident: Many glaciers are now shrinking rapidly, vegetation productivity has increased, and birch forest boundaries are moving upward (Björnsson 2009).

Hence, due to its almost pristine land open for experimentation and its position in a part of the world, Arctic and Subarctic, recognized to be extremely sensitive to climate change, Iceland offers a

unique opportunity to study the behavior of species outside their distribution and observe how they will respond to further changes. Also, a country like Iceland, where natural immigration of trees is almost impossible, enables investigation of strategies such as assisted migration as valid opportunity for tree species to cope with climate change.



*Figure 1. Distribution of forests and woodlands in Iceland. Taken from "*Spatial Distribution of Forests and Woodlands in Iceland in Accordance with the CORINE Land Cover Classification." (*Traustason and Snorrason 2008*).

1.5. Analyzed species

The species on which this research focuses is *Picea abies* (L.) H.Karst., a key species for economic and environmental reasons, with a very wide distribution, as reported in figure 2. Its native range spans from up above the Arctic Circle, creating a large continuum (Scandinavia, Siberia, Baltic States, Poland, Belarus), to the mountain chains of Southern Europe (Italy, Balkanic States); in the West-East direction the species can be found starting from Norway in the west and reaching the Ural Chain in the European Russia, where it merges with Siberian spruce (*Picea obovata* Ledeb.) (Scotti et al. 2000; Aarrestad et al. 2014; Caudullo, Tinner, and Rigo 2016). It was also introduced in other countries outside Europe (United States, Canada and Japan) and in the southern hemisphere (South Africa, Tasmania and New Zealand) (Caudullo, Tinner, and Rigo 2016). Norway spruce has been cultivated and favored over long periods by forest managers, especially in the lowlands (Fennoscandia, Central Europe), but also in mountain areas (Italy, Austria, Switzerland) bringing it to the limit of its ecological niche (Scotti et al. 2000; Caudullo, Tinner, and Rigo 2016).



Figure 2. Plot distribution and simplified chorology map for Picea abies. Taken from "Picea Abies in Europe: Distribution, Habitat, Usage and Threats." (Caudullo, Tinner, and Rigo 2016)

As support to the study and to better understand growth dynamics occurring in the Icelandic sites, we decided to collect also samples from other tree species. We focused on two of the main species adopted in Icelandic silviculture (Blondal 1987; Snorrason and Kjartansson 2017): *Picea sitchensis* (Bong.) Carr. and *Pinus contorta* Dougl. ex Loud.

Relatively rare in Europe but commercially very important in some countries (United Kingdom and Ireland) (Houston Durrant et al. 2016), Sitka Spruce is native to the west coast of North America, where it grows in a narrow strip along the north Pacific coast,

from southern Alaska to northern California (Harris 1990; Mimura and Aitken 2007; Houston Durrant et al. 2016) (figure 3). In Europe this species was introduced in the 1800s and it is now planted in more than 16 countries worldwide (Houston Durrant et al. 2016). As reported in figure 4, the majority of plantations are in the United Kingdom (25 % of the national forest area) and Ireland (52 % of national forest area) but it is also important in Denmark (Houston Durrant et al. 2016). At the beginning of the twentieth century Sitka Spruce has also been planted in Norway and Iceland (Houston Durrant et al. 2016), where



*Figure 3 (left). Distribution of Picea sitchensis among its native range, along the north Pacific coast. Taken from "*Sitka spruce in Great Britain: wood properties and uses" (*Moore 2011*).

*Figure 4 (right). Plot distribution and simplified chorology map for Picea sitchensis in Europe. Taken from "*Picea sitchensis in Europe: Distribution, Habitat, Usage and Threats." (*Houston Durrant et al. 2016*).

nowadays it represents one of the main species used in the island (Blondal 1987; Snorrason and Kjartansson, 2017).

The other supporting species, lodgepole pine, is an ubiquitous species, growing throughout the Rocky Mountain and Pacific coast regions, extending north to the Yukon Territory (lat. 64") and south in Baja California (lat. 31"), and west to east from the Pacific Ocean to the Black Hills of South Dakota (Lotan and Critchfield 1990) (figure 5). Due to its economical relevance and its wide ecological amplitude, it has also been planted outside its native range all around the world. Forests of lodgepole pine can be found in Great Britain, Ireland and Russia, where is considered naturalized; and in Australia, New Zealand, Sweden, Chile and Argentina, all countries where the species is considered invasive (Langdon, Pauchard, and Aguayo 2010) (figure 5). In Iceland this species covers 11% of the forested area and, as well as Sitka Spruce (Snorrason and Kjartansson, 2017), it now represents one of the most important tree species.

Alongside the study of the distribution and the ecological features of these species, to ensure a proper development of the established forests it is fundamental to select the seed provenance. This can also lead to a better understanding of growth response and adaptation to climate. Regarding Iceland, given the need for the most appropriate ecotype for the successful plantation in harsh climates, the seed collected for the analyzed sites comes from a broad range of Countries. As reported from the Icelandic Forest Service, the seed sources are Skagway area (Alaska) for Sitka spruce and Lodgepole pine, and Trysil and Rana (Norway) for Norway spruce. Regarding Italy, the seed used to establish the studied Norway spruce plantations most likely comes from southern Alps, where there are similar conditions to the Apennines' plantation sites analyzed in this project.



Figure 5. Global distribution of Lodgepole pine, inside (throughout the Rocky Mountain and Pacific coast regions of North America) and outside (Great Britain, Ireland and Russia, Australia, New Zealand, Sweden, Chile and Argentina) its natural range. Taken from "Pinus Contorta Invasion in the Chilean Patagonia: Local Patterns in a Global Context." (Langdon, Pauchard, and Aguayo 2010)

These species, among the sites chosen for the analysis, are found to be outside their natural range. In particular, in Italy, *Picea abies* plantations located in Marche Region is found to be just outside Norway spruce's southernmost distribution limit, which is located in the northernmost part of Apennines range (Appennino Tosco-Emiliano) in the area of Campolino (44°07' N, 10°42' E), (Di Pierro et al. 2016).

They can be defined as introduced species, given the fact that there are just small population of established adult plants beyond their previous geographical range (Richardson et al. 2000) without, so far, the environmental/ecological conditions for them to spread without control (Ricciardi and Cohen 2007; Lodge et al. 2006; Hellmann et al. 2008). The only exception is lodgepole pine, which, due to its pioneer attitude, seems to be naturally regenerating and fast spreading across Iceland. This stimulating a strong debate among forest owners and the Icelandic Forest Service on whether it should be considered as an invasive exotic species or not (Guðmundsdóttir 2012). In fact, as reported in many other countries outside its natural range as New Zealand and Chile (Langdon, Pauchard, and Aguayo 2010), in the future it could spread without control and therefore threat native plant species.

2. MATERIALS AND METHODS

2.1. Field work

2.1.1. Study area

In Iceland samples have been collected in four different sites, in order to have a picture of the multiple conditions that can be found in the island. We collected Norway spruce samples in two sites (Hallormsstaður and Vaglaskógur), while, in order to support and better understand growth responses to climate, we also collected Lodgepole pine in one site (Steinadalur) and Sitka spruce samples in another one (Rauðavatn). In Italy, the samples were collected in two sites in the Apennines Range, from Norway spruce plantations located in correspondence (Trefiumi) and beyond (Fonte Abeti) the southern distribution limit of the species, located in Campolino, (44°07′N, 10°42′E) (Scotti et al. 2000). For each of them a complete description in the following chapter is provided.

• Site 1, called Rauðavatn and identified by the label 000R1, is located right outside the city of Reykjavik, on the eastern side (64°06'14.63"N, 21°45'46.15"W, 80 m a.s.l). Rauðavatn is more correctly the name of the lake around which the forest growths, which literally means "Red Lake", due to the presence of aquatic perennial plants with reddish stems. Some areas of this forests represent the remnants of the first tree nursery with forestry purposes created around 1900 and now left.

The forest is divided in two main plantations, one of lodgepole pine and one of Sitka spruce. The Lodgepole pine plantation (*Pinus contorta* Douglas) is naturally regenerating at a high rate, faster than the Sitka spruce, closing the 20/30 meters gap between the stands. In the surroundings, typical native birch (*Betula pubescens* Ehrh.) formations can be found, presenting high tree density, with a mean height of 2-3 meters. The Sitka spruce plantation selected for the study dates to roughly 1950 (IFS report 1948 as the exact year), making it one of the first plantation in Iceland. The seeds were imported from Skagway area, located in the south of Alaska, USA. The forest presents a high density (95 – 100% coverage), without any ground vegetation, with the forest floor almost completely covered by dead needles. The overall health condition appears good, even though the crowns are small due to the high density. Initial density after planting was ca. 4000/4500 seedlings/ha (1.5*1.5 m); after 1 selective thinning, conducted roughly 25 years ago (1995), today the average density results around 800/900 plants/ha (3.5*3.5 m). We collected samples for a total of 18 Sitka spruce trees.

• Site 2 is called Steinadalur and it is identified by the label 000S2. The name of the site coincides with the name of the valley in the South Eastern part of Iceland where the sampled forest is

located (64°10'04.44"N 15°59'45.61"W, 50 m a.s.l.). The plantation, rising on the foot of Mount Staðarfjall (max elevation 928 m a.s.l.), was established in 1954 and it is located just over 4 km from the ocean (Guðmundsdóttir 2012). The rocky part and the slopes of Mount Staðarfjall are sparsely vegetated mostly with native *Betula pubescens* (figure 6). The plantation initially had an area of 0.4 hectares; which was extended to cover 2 hectares in 1961 (Guðmundsdóttir 2012).



Figure 6. West view of Steinadalur plantation and Mount Staðarfjall. It is possible to see the widespread presence of Lodgepole pine natural regeneration, which spans from the slopes of Mount Staðarfjall to Steinadalur plane (Author 2020).

In 1959 the first 300 Lodgepole pine seedlings coming from the Hallormsstaður seedbed (seed provenance: Skagway area, Alaska) were planted; in 1965 and 1969 a total of other 1250 plants of the same species were planted (Guðmundsdóttir 2012). In addition to Lodgepole pine, in the years 1954-1969, *Pinus silvestris, Larix sibirica, Picea abies, Picea sitchensis* and *Pinus aristata* were also planted (Guðmundsdóttir 2012). In 1985, a first natural regeneration wave were identified, arriving to observe in 1992 the presence of mature cones and to spot in 2007 the presence of a seedling at an altitude of 300 m a.s.l. and over 1 km away from the forest (Guðmundsdóttir 2012), testifying the pioneer behavior and the colonizing ability of this species. Nowadays, the forest looks mature, with a crown cover of more than 90% and a ground cover of 100%, mostly made of dead needles. The density stands at around 800/900 plants/ha (3.5*3.5 m). For the analysis, 15 lodgepole pine trees were sampled.

• Site 3 located into Hallormsstaður forest, close to Egilsstaðir (East Iceland, 65°07'21.31"N, 14°41'04.03"W, 126 m a.s.l) is identified by the labels 000H3 and 00HT3 (*T* stands for *thinned*). As reported by the Icelandic Forest Service, which is also the owner, this forest is one of Iceland's biggest forests (740 ha), originally one of the last big birch woodland in Iceland saved from eradication at the turn of the 20th century. Since 1905, the forest has been the site of large-scale trials of exotic species, such as *Larix sibirica, Picea abies, Picea sitkensis, Picea engelmannii, Larix sibirica* and *Tsuga mertensiana*.

The area of the plantation selected for the analysis consists of a mixture of *Picea abies* L (95%) and *Pinus contorta* Douglas (5%) (figure 7). The planting goes back to 1956, with the seed source located in Trysil, Norway. Most of the forest is quite dense, reaching a coverage of 90%. The ground vegetation coverage is 100%, with presence of moss, *Rubus saxatilis*, mushrooms. Tree crowns are quite small, due to density, but overall health conditions are good. Gaps in the forest cover have been generated by some lodgepole pine individuals subjected to windthrow. In some of these gaps it is possible to find the presence of Norway spruce

regeneration (figure 8). A small area of the forest presents a lower density (20%) and mixed composition made by Siberian larch and Norway spruce. The crowns appeared full and very healthy. Ground cover was about 100%, made mostly of grasses, which prevent the establishment of regeneration. Here, the standalone trees, especially Picea abies, could reach bigger dimension, both in diameter (up to 38 cm) and height (up 19.2 m), due to lack of competition. In the denser part of the forest one very light pre-commercial thinning was conducted roughly 20 years ago (2000), followed by pruning to increase wood quality. That brought the 1200/1300 average density at ca. plants/ha (2.8*2.8 m) today, where in the rest of the forest it is at ca. 2000 plants/ha (2*2.5 m). Here, due to a lighter crown coverage, the forest floor is made of moss, Rubus saxatilis, Vaccinum myrtillus, Betula pubescens, herbs, mushrooms and



Figure 7 (above). View of the thick Norway spruce stand chosen for the analysis. (Author 2020) Figure 8 (below). Presence of Norway spruce regeneration in natural gaps (Author 2020).

sparse presence of *P. abies* regeneration. We sampled a total number of 24 *Picea abies* trees, with 10 trees chosen from the thinned part of the forest, in order to have a picture of the different growth trends in the last 20 years.

Site 4 located into Vaglaskógur forest in Fnjóskadalur (North Iceland, 65°42'26.77"N, 17°53'13.75"W, 163 m a.s.l) is identified by the label 000V4. Vaglaskógur is one part of the largest continuous forest in Iceland which covers most of the eastern valley side south of Ljósavantsskarð pass (IFS), hosting a large number of plantation made of species such as Lodgepole pine, Engelmanni spruce, Siberian larch and Norway spruce and a widespread birchwood conservation area, which spans about 690 ha (IFS).

The plantation area chosen for the analysis is composed of *Picea abies* (95%) and *Pinus contorta* (5%) (figure 7). The planting dates to 1948-1954, with the seed source located in Rana, North Norway (IFS). The forest is dense, with a crown coverage of 85–100%, and a ground vegetation coverage of 100%, with presence of moss, *Rubus saxatilis, Vaccinum myrtillus, Calluna vulgaris, Betula pubescens*, herbs and mushrooms. In a small portion in the higher part of the

stand, a thinning has been operated, followed by pruning to increase wood quality. This operation has been done maximum two years ago and during the analysis this has not been considered, inasmuch the intervention is too recent and not detectable in the growth trend. The thinning brought the average density at ca. 4000/4500 plants/ha (1.5*1.5), whereas in the rest of the forest the density remains higher. A total of 23 Norway spruce trees have been sampled in this site.

- Site 5 is located in a forest belonging to an agro-forestry company called "Fonte Abeti" (Marche Region, Italy. 43°35'55.9"N 12°13'37.5"E, 970 m a.s.l.). The company is part of a SIC (Site of Community Importance) called "Alpe della Luna e Bocca Trabaria", situated in the central Apennines Range, between 550 and 1252 m a.s.l. The site is identified by the label FABPA. The analyzed plantation is mainly composed of Silver fir (Abies alba), covering a small valley located in the north slope of Poggio del Romito (border between Umbria, Toscana and Marche Regions) for a total of 15 hectares (Sangermano 2012). After being over-exploited during World War I (1915-1918), the natural Silver fir forest have been repopulated through natural regeneration, with the seed coming from the remnant silver firs, and through planting of silver fir and other species, such as Norway spruce and Greek fir (Abies cephalonica) (Sangermano 2012). Some interventions have been made by the State Forest Service (Corpo Forestale dello Stato) between 1982 and 1987, consisting of additional plantings, forest floor cleaning and logging of some individuals (Sangermano 2012). A total of 15 samples have been collected in August 2020 by prof. Marco Carrer (TeSAF Dept.). Moreover, to assamble a longer and stronger series 34 samples collected for the thesis work "Dinamismi di accrescimento e sensitività climatica in una cenosi di abete rosso (Picea abies) della Massa Trabaria (PU) by Pietro Sangermano (2012) have also been added. These samples are identified by the label F3PA.
- Site 6 (Norway spruce) is located in the northern section of Appennino Tosco-Emiliano National Park (Emilia Romagna Region, Italy, 44°23'03.4"N 10°06'23.2"E, 1100 m a.s.l.), near the border between Toscana and Marche Region, on the northern Apennines range. The sites location, close to Campolino, coincides with the southernmost limit of Norway spruce's natural distribution. The vegetation includes large beech forests sometimes mixed with silver fir and Norway spruce, that, as reported, has its southernmost presence here in Italy, relict stations of Mediterranean formations over a thousand meters and high-altitude grasslands with endemic botanical species. A total of 16 samples from Norway spruce trees have been collected in August 2020 by prof. Marco Carrer (TeSAF Dept.). The samples are identified by the label TREPA.

The location of the sites is reported in figures 9 and 10, as long as Norway spruce distribution range (both natural and introduced) and limits. The maps have been created using QGIS software (version 3.10.0).



Figure 9 (above) and 10 (below). Localization of the analyzed sites in Iceland (fig. 9) and Italy (fig. 10). The labels report the initials and the number of the sites. It is possible to see the position of Italian sites (F5 and T6) in respect of Campolino, the recognized natural southern distribution limit of Norway spruce in Italy.

Legend

- Sites localization
- Campolino
- Picea abies Natural distribution range
- Introduced and naturalized
- Introduced and naturalized isolated population

2.1.2. Field sampling

Icelandic samples were collected using an increment borer roughly at knee height (50 cm), in order to extend, as much as possible, the length of the series. Two samples for each tree have been collected, while just one on trees with a dbh smaller than 18-20 cm. We tried to select the oldest trees, considering mainly tree dimension and bark aspect. We tried to have a thorough picture of the stand: the selection focused randomly on edge and inner trees, stand interested or not by thinning, standalone trees. For each site the core samples have been stored inside plastic straws, with a label consisting of an 8-digitcode, providing site information (site initial and site number) and the sample number. Sometimes other info has been included in the ID code, such as species (e.g. PA=Picea abies) or thinning (T). Within sites R1, H3 and V4, height and dbh (or circumference at breast height, then converted into diameter) have been measured and reported for each tree. All information has been reported in excel (location, date, site condition, seed provenience).

The Italian samples were collected by prof. Marco Carrer and his team (TeSAF Dept.) through increment borer at breast height (1.30 m). One sample for each tree has been collected, focusing on the oldest individuals. Each sample was glued to a wooden support in order to keep it safe. Again, the label consisted of an 8 characters code, providing site initials, species identifications (PA=Picea abies), and sample number. The 34 samples coming from Sangermano's (2012) thesis work were collected in 2012 and stored with the same procedures. In this case the 8 characters code consisted of site and plot information (F3 in this case), species information (PA=Picea abies), number of the sample and direction of sampling (M=Monte (upstream), D=Destra (right), S=Sinistra (left)). For Italian sites height and dbh measures are not available.

2.2. Analysis

2.2.1. Samples processing and measuring

Once the samples dried, they were prepared for the dendrochronological analysis. The upper part has been cut away or cleaned using sandpaper, to get a smooth surface where the rings could be clearly identified. After this, each sample has been analyzed using LINTAB and the software TSAP (TSAP-win, Rinntech) (figure 11). LINTAB is a digital positioning table for tree-ring analysis, where the measuring stage is a linear encoder (precise to 0.01 mm) hooked to the measurement capture button, which is connected to the computer through USB or serial port connector. LINTAB is compatible with TSAP, a software that allows to save and process tree-ring measurements. Thanks to these devices it has been possible to measure age and ring width, and to create a table that describes the progression of these parameters. In case of the presence of two cores per tree a mean series was created. Afterwards, an average series for each site has been calculated, in order to create a table representing the growth trend and event rings, which are consistently narrow or have peculiar characteristics over years (Speer 2010). The work on the table and the creation of the average series has been made directly on TSAP.



Figure 11. Workstation at the dendro lab of the Icelandic Forest Research, division of the Icelandic Forest Service (Skógræktin), in Mógilsá, Reykjavik. Particular of the digital positioning table LINTAB (Author 2020).

2.2.2. Crossdating

The cross-dating has been evaluated using the programs COFECHA (Holmes 1983) and ARSTAN (Cook and Holmes 1997), which provide a statistical match between segments of each core and a master chronology made of the measurements that are entered into the program (Speer 2010). COFECHA, firstly standardized each series using a 32-year cubic spline, with 50% frequency response at a wavelength of 32 years, that is usually considered the best spline length for enhancing the interannual variability to eases the control for a correct dating (Speer 2010; Grissino-Mayer 2001). After fitting the cubic smooth spline to the cores, the program creates a master chronology by averaging all of the index series for all of the cores together (Speer 2010). The core that is about to be analyzed is afterwards removed and cut it into 50-year segments with 25 years of overlap; Therefore, the program statistically correlates each segment against the master chronology (Grissino-Mayer 2001; Speer 2010). If the correlation is below a specified confidence level (99% by default), then COFECHA checks from -10 to +10 lag years for a better match. If a better match is found the program reports a B flag in the output, whereas, if it does not, it reports an A flag highlighting a low correlation (Speer 2010). All the tree series with a correlation (r) with master series lower than 0.300 or with a B flag have been re-measured, thoroughly checked in order to get better matches with master chronology or eliminated, in order to try to get a final series intercorrelation as high as possible.

Once the series have been fully checked and corrected, they have been standardized with ARSTAN, which has many similarities to COFECHA, but differs in the fact that it has a broader

range of standardization techniques that can be used on individual series before complying the master chronology (Speer 2010). In this case, it used a 50 years-cubic spline, with 50% frequency response at a wavelength of 50 years. This has been done in order to compare different flexibility of the splines and therefore to see how the output would change and how the correlation with climate would subsequently vary. ARSTAN has also been used with the purpose of getting a standardized chronology for each tree (feature not provided by COFECHA), in order to possibly analyze the growth response to climate at tree level. After the single tree series have been produced by the program, the average standardized index has been reported to compare the whole site's average standardized growth with the growth index created by COFECHA and subsequently with climate variables.

Finally, to compare each site chronologies, several descriptive statistics commonly adopted in dendrochronology have been used. These statistics included the number of cores (N), the length of the master series (L), the mean ring width (MRW), the mean sensitivity (MS) and standard deviation (SD) to assess the high-frequency variations (Fritts 1976), the first-order serial autocorrelation (AC) to detect eventual persistence retained after the standardization, the mean correlation between trees (rbt) and) and the expressed population signal (EPS)(Carrer and Urbinati 2004; 2006; Carrer et al. 2010).

2.2.3. Climate data

Climate data (monthly precipitation and temperature series) for the Icelandic sites have been downloaded from the website of the Icelandic Meteorological Service. The station data were as close as possible to the studied sites in order to represent at best the local climate, in particular:

- Reykjavik (Rauðavatn, site 1), manned synoptic station (ID: 1, WMO number: 4030) located in Reykjavík (SW Iceland, 64°07'38.9"N 21°54'10.0"W, 52 m a.s.l) (Icelandic Meteorological Office). Series are from 1920 to 2019
- Höfn í Hornafirði (Steinadalur, site 2), Automated observational station (ID: 5544, WMO number: 4082) located in Höfn í Hornafirði, (SE Iceland, 64°16'08.7"N 15°12'48.7"W, 5.0 m a.s.l.) (Icelandic Meteorological Office). To complete the climate series, we also used the nearby stations of Akurnes and Hjardarnes, by simply adding lacking data to the series. Series from 1965 to 2018
- Egilsstadðir (Hallomstaður, site 3), synoptic station (ID: 571, WMO number: 4089) located in Egilsstaðaflugvöllur, (E Iceland, 65°16'58.8"N, 14°24'09.0"W, 23.0 m a.s.l.) (Icelandic Meteorological Office). To complete the climate series, we also used another nearby station (ID 4271), by simply adding lacking data to the series. Series from 1954 to 2019.
- Akureyri (Vaglaskogur, site 4). manned synoptic station (ID: 422, WMO number: 4063) Akureyri (NE Iceland, 65°41'08.1"N, 18°06'00.8"W, 23.0 m a.s.l) (Icelandic Meteorological Office). Series from 1949 to 2019.

For the Italian sites the situation is more complex, due to the lack of data sources close to the sites. Monthly temperature and precipitation series, covering a period that spans from 1880 to 2018, have been reconstructed as explained in the works of Carrer, Brunetti, and Castagneri (2016) and Carrer et al. (2019) by exploiting the observational weather data available for the Apennines region through the anomaly method technique described in Brunetti et al. (2012). The interpolation procedure consists of the independent reconstruction of the climatologies, such as the climate normals over a given reference period, and the deviations from them (i.e. anomalies) (Carrer, Brunetti, and Castagneri 2016; Carrer et al. 2019). Climatologies have been reconstructed with an interpolation technique that considers the local dependence of the meteorological variable on elevation (Brunetti et al. 2014; Crespi et al. 2018), requiring at the same time a high spatial density stations network, even when data are available for only a limited temporal period (Carrer et al. 2019). Anomalies, being linked to climate variability, show a higher spatial coherence and therefore a simpler interpolation technique and a lower spatial density of stations are enough to reconstruct them (Carrer et al. 2019). However, a long temporal coverage and accurate homogenization of the data time series are of fundamental importance (Carrer et al. 2019). Lastly, the superposition of the two fields, representing climatologies and anomalies, provides monthly temperature and precipitation series in absolute values for the analyzed sites (Carrer et al. 2019). Information about the techniques and their accuracy are provided in Brunetti et al. (2012, 2014) and Crespi et al. (2018). The two climate records are:

- Fonte abeti (site 5). Data reconstructed for the coordinates 43°35'55.9"N 12°13'37.5"E, 970 m a.s.l. Series from 1880 to 2018
- Trefiumi (site 6). Data reconstructed for the coordinates 44°23'03.4"N 10°06'23.2"E, 1100 m a.s.l. Series from 1880 to 2018.

Starting from these climate series it has been possible to create climographs (Graph 1, A-F) for each site, in order to have a picture of the different climate regimes.







C) Average T: 3.43 °C Total Precipitation: 612.37 mm



E) Average T: 9.72 °C Total Precipitation: 1366.20 mm





B) Average T: 4.65 °C Total Precipitation: 1413.92 mm



D) Average T: 3.71 °C Total Precipitation: 521.17 mm



F) Average T: 7.94 °C Total Precipitation: 2249.15 mm

Graph 1 (A-F). Climographs relative to the analyzed sites, created using the available climate data (average monthly precipitation and temperature series). It is possible to appreciate the precipitation distribution, presenting one peak over the year for Icelandic sites (A,B,C and D) coinciding with Winter months; and two peaks for Italian sites, the first at the beginning of spring and the second, more pronounced, during fall months (E and F). Total precipitation amounts are quite heterogeneous, either between the Icelandic sites, spanning from roughly 520 mm (Akureyri, D) to 1400 mm (Höfn í Hornafirði, B), and the Italian sites, spanning from roughly 1360 mm (Fonte Abeti, E) to more than 2200 mm (Trefiumi, F). However, the monthly precipitation regime within each Icelandic site is quite homogeneous (apart for Höfn í Hornafirði, B), according to the oceanic nature of Iceland climate. Regarding the temperature values, the variation between Icelandic and Italian sites is quite pronounced, with the average year temperature being to roughly 4 °C and 8 °C, respectively. An important driver for Italian sites climate condition is their location on the Apennines Range, which can heavy influence local precipitation amount and temperature values.

2.2.4. Climate-growth relationships

The analysis of the climate-growth relationships has been performed using the standardized growth indexes, which removed the age/size effect in ring width dimension that is the effect of autocorrelation, or the correlation of a variable with itself over successive time intervals (Speer 2010). Therefore, these indexes have been contrasted with climatic variables such as mean summer temperature, mean summer precipitation and monthly temperature and precipitation values to find the best possible correlation between each site and every month's precipitation and temperatures averages has been compared, using different standardized series to see which month's data gave back the best correlation with each site's growth index.

To assess climate-growth relationships between site chronologies and monthly climate data, the Pearson correlation was calculated. The significance threshold has been set utilizing the critical values for correlation coefficient. The correlation has been calculated between chronologies and average monthly temperatures and precipitations values (summer and monthly average) over the period of 52 years from 1967 to 2018, based on climate data availability and series length. Climate-growth relationships have been analyzed from June of the previous year through September of the year of growth, to see if previous year climate would be able to influence the following year's growth. Moreover, thanks to ARSTAN outputs, which creates single standardized series for each tree, it has also been possible to compare each individual tree responses to climate. This has been made for each site separately, to analyze the dynamics occurring within the sites.

3. RESULTS

3.1. Chronologies descriptive statistics

The correlation between indexed chronologies and climate data was higher with the indexed chronologies created fitting the 20-year cubic smoothing spline. This kind of flexible spline curves was more efficient in removing both the long-term trend and the effects of localized disturbance events and therefore in extracting the climate signal, but at the risk of removing possible low-frequency climatic information (Cook et al. 1990). Statistics of raw and indexed chronologies are summarized in Table 1. After the elimination of the low-crossdated tree-ring series, highlighted by COFECHA, the resulting 134 trees have been used to compute the tree-ring chronologies. Those span from 53 to 95 years and have a mean treering width ranging from 1.73 to 3.69 mm. Mean sensitivity (MS) and tree-ring width standard deviation (SD) vary from 0.069 to 0.173 and 0.075 to 1.7 respectively. The significance of mean tree-ring width and mean sensitivity variability between the sites has been confirmed by the analysis of variance (ANOVA) conducted on these parameters, as showed in the results reported in table 2. After the standardization, all except two site chronologies (S2 and TREPA) reach the minimum EPS value of 0.85, a widely used threshold in dendroclimatic studies. This demonstrates an overall strong climate signal in most site chronologies. All sites exhibited a high serial autocorrelation in their mean raw chronologies, demonstrating a strong dependence of current growth on the previous year's growth. A significant amount of autocorrelation has been afterward removed through the standardization process. The mean indexed series are illustrated in graph 2 (A-F), where it is possible to appreciate the different interannual growth variability, which vary significantly within all sites (especially FABPA) except S2, which is more complacent.

	Ν	L (years)	MRW (mm)	N	15	S	D	AC	(1)	Mear	rbar	El	rs
R1	17	62	2.57	0.202	0.16	0.945	0.167	0.826	0.148	0.478	0.344	0.94	0.899
S2	12	53	3.69	0.083	0.069	0.867	0.075	0.877	0.286	0.597	0.331	0.942	0.844
H3	24	56	2.39	0.203	0.173	0.731	0.17	0.694	0.202	0.655	0.556	0.964	0.964
V4	22	56	1.73	0.175	0.15	0.397	0.15	0.644	0.173	0.3	0.536	0.794	0.912
FABPA	48	95	2.64	0.19	0.171	1.291	0.163	0.834	0.185	0.273	0.322	0.818	0.851
TREPA	11	70	3.20	0.135	0.119	1.547	0.139	0.925	0.34	0.574	0.271	0.937	0.803

Table 1. Descriptive statistics for each site tree ring chronologies. Chronology statistics include mean ring width (MRW) standard deviation (SD), first-order serial autocorrelation (AC), mean sensitivity (MS), mean interseries correlation (rbar), and expressed population signal (EPS) computed on the indexed tree-ring series. All statistics have been computed with raw tree-ring series, except the ones highlighted in bold that derived from indexed series.

	SS	df	MS	F	P-value	F crit
MRW	38.13058897	5	7.626117794	19.49860017	2.57235E-13	2.310224845
MS(indexed)	0.25183409	5	0.050366818	40.89148533	3.02104E-25	2.282856163

Table 2. ANOVA (analysis of variance) results for mean tree-ring width (MRW) and indexed mean sensitivity (MS) variation between the sites.



Graph 2 (A-F). Mean indexed chronologies for the analyzed. Norway spruce chronologies are illustrated in graphs C, D, E, F. The chronologies have been created using a 20 year-cubic spline, with 50% frequency response at a wavelength of 20 years.

3.2. Growth dynamics comparison

Analyzing tree-ring width chronologies several different trends emerged, regarding both the dynamics occurring among the sites and the species-specific behaviors. Focusing on Iceland sites, the species demonstrate a homogeneous overall growth pattern as reported in graph 3A, especially regarding sites H3 and V4. Sites R1 and S2 still present a similar growth pattern however they also show some differences in the pointer years and a significant increase in ring width along two decades, 1970 and 1980. Going in detail, within the sites a significant drop in ring width occurs in 1993 and 1998 (except for R1) and in 2011 and 2015. On the other hand, a positive peak in ring width is shown in 1984, especially for S2, H3 and V4. Therefore, despite the distance among sites, climate and various disturbances dynamics are likely the key drivers able to simultaneously affect tree-ring growth variability across the whole island. This is true especially for Norway spruce which shows, for sites H3 and V4, very high similar growth variability. In Italy, as visible in graph 3B, growth patterns are more different between the two sites, with significant common pointer years occurring just in 1997. Therefore, despite the rather short distance and



Graph 3 (A-C). Tree-ring width chronologies for Icelandic sites (A), Italian sites (B) and for Norway spruce (C)

the similar mountainous context, the drivers affecting Norway spruce in the Apennines appears quite different. Finally, in graph 3C, it is possible to appreciate the comparison between all the Norway spruce growth patterns. They show similar growth trends and rate despite their setting beyond the species natural distribution range, condition that theoretically should strongly influence tree performance.

3.3. Climatic influences on tree growth

The correlation profiles of each site show that the influence of climate on growth changes according to latitude: in Iceland, it is mainly associated to temperature and is concentrated in a 4-month period from May to August; in Italy it relies more on precipitation. Particularly, significant correlation occurs between Norway spruce growth and current year summer temperatures in Icelandic sites (especially June, July, August), showing the strong driving force of the heat amount on tree growth in the northern sites. Sitka spruce appears to be less limited to current year's summer temperatures, presenting significant correlation only with July temperatures, whereas it seems to be mainly negatively influenced by previous year's summer temperatures (June-August). Lodgepole pine presents an even different



Graphs 4 and 5. Climate-growth associations among monthly mean temperature (4) and precipitation (5) and site ring-width indexed chronologies. Climate variables (1967–2018) have been considered for the previous (June to December) and current (January to September) growth-year months. The correlation is coded according to the color scale on the bottom of graph 5. Values above |0.2732| are significant at p < 0.05 while values above |0.3542| are significant at p < 0.01.



Graph 6. Climate-growth associations among Summer (June, July and August) mean temperature (4) and precipitation (5) and site ring-width indexed chronologies. Values above |0.2732| and |0.3542| are significant at p < 0.05 and p < 0.01, respectively. correlation profile, being significantly influenced only by current year's May and July temperatures. On the southern front, Norway spruce in the Italian sites shows weaker correlation with temperature, with significant negative correlation only in FABPA for current year July temperature.

Regarding precipitation, the correlation profile is weaker and varies consistently between sites. Icelandic sites present weak correlation between growth and precipitation regimes, with the significance threshold reached only by Sitka spruce (S1), showing high correlations especially with previous year August to October (positive) and November (negative) and current year April precipitation. Moreover, Norway spruce located in site H3 shows significant negative correlation with current year's May and lodgepole pine at site S2 shows the same negative correlation with previous year's November. Norway spruce in Italy shows an overall stronger correlation with precipitation, especially at FABPA, although the significance threshold is reached only within previous year's June and current July. Norway spruce at TREPA presents significant correlation only with current year January.

A more detailed analysis on correlation between growth and mean summer (June, July and August) temperature and precipitation, corroborated the previous results. It shows an even stronger correlation between temperature and growth, with the significance threshold reached by site S2, H3 and V4 confirming the relevance of summer temperature as a driver for tree growth in Iceland. On the other hand, Italian sites (FABPA and TREPA) shows a weakening of the correlation, which does not reach the significance threshold. Summer precipitation has confirmed its marginal role in tree development except, as previously showed, for Norway spruce in site FABPA.

Concluding, Norway spruce seems to respond differently to temperature and precipitation beyond the limits of its distribution. In Iceland the main driver is summer temperature whereas precipitation plays a minor role, as it is not a limiting factor; in Italy, growth seems to be more related to previous and current year's precipitation regimes, especially for site FABPA, where higher temperature starts to be even unfavorable in summer months, as shown by the negative correlation.

4. DISCUSSION

The aim of this thesis was to investigate the growth-climate relationships of Norway spruce beyond its natural distribution range through a dendrochronological approach, in order to assess the adaptation of the species to current climate change and to the future conditions they can possibly face. Temperature and precipitation are in fact among the major ecological variables that determine plants' natural distribution and drive their adaptation. Therefore, by studying the climate/growth associations we could have a better understanding of trees' growth patterns, especially in a warming climate context. Moreover, the inclusion in the study of Sitka spruce and lodgepole pine plantations has proved useful to understand the complex dynamics that govern the relationship between climate and growth, especially in areas that are outside the natural distribution of a species.

4.1. Growth patterns: characteristics and drivers

The descriptive statistics for the chronologies reported in table 1 shows several species-specific and site dependent peculiarities that allow us to identify the different responses of trees to climate. First, mean tree ring width for Norway spruce, which spans from 1.73 and 2.39 mm (V4 and H3) to 2.64 and 3.20 mm (FABPA and TREPA), demonstrate an overall low, yet significant, difference between Icelandic sites and Italian sites. On the other hand, standard deviation, which expresses the variability of growth, shows higher differences, being smaller in the Icelandic sites (0.731 in H3 and 0.397 in V4) partially due to thinning procedures, especially in site H3, and in general to a steadier growth. The effect of thinning on site H3 is identifiable also in tree ring width chronology (graph 3A) where, after a negative event year in 2002, which roughly matches with the year of thinning (IFS), the growth trend shows a substantial inversion, testifying a positive increment in tree growth due to the greater availability of resources. Standard deviation is much higher in the Italian sites, possibly attributable to an high precipitation variability (standard deviation calculated for averaged precipitation records within the common period 1967-2018 sets at 288.9 mm for Italian sites and at 104.8 for Icelandic sites), which can strongly influence growth, especially towards southern latitudes. Mean sensitivity (MS) and first order autocorrelation (AC(1)) are the parameters that express the response to endogenous and exogenous perturbative factors occurring at different frequencies (Speer 2010). As a result of this analysis Norway spruce can be defined as a low to medium sensitive species since the MS (indexed) sets on average at 1.53, expressing a discrete reactivity of the species to climatic variability, which acts at high frequency. The autocorrelation related to the raw series assumes low values in the Icelandic sites (0.69-H3; 0.64-V4) indicating a greater sensitivity of the species to the factors that act in the short term (climate) in respect of Italian sites, where AC is much higher, showing a higher sensitivity in the medium-long term and therefore an overall lower influence of climatic variability. Hence, there is a substantial difference in the behavior of Norway spruce between Iceland and Italy. This could be linked to the location of Icelandic Norway spruce far outside its optimal range, at the ecological limits for the species, especially for Icelandic sites, making it more sensitive as changes in local climatic conditions can limit its growth. It is also important to specify that

Norway spruce presents continental tendencies whereas Iceland climate is classified as Oceanic (Einarsson 1984; Hanna, Jónsson, and Box 2004), fact that could further explain is higher sensitivity to climate variability. This is less pronounced towards and beyond the southern limit of its distribution, within the Italian sites, where the two plantations are still likely within an optimal climate niche for Norway spruce. Here however, as shown by the high values of standard deviation, the species is still quite sensitive to precipitations regime fluctuation, showing the main limit of this portion of the distribution, moisture. Moving to the support species, Lodgepole pine and Sitka spruce statistics present low values of indexed MS and medium to high values of raw AC(1), probably due to their broader ecological amplitude (Lotan and Critchfield 1990; Houston Durrant et al. 2016). The only noticeable difference is with Lodgepole pine MS, which is 0.069, expressing a low reactivity of the species to climatic variability. This fact is still attributable to its wide ecological amplitude and pioneer attitude (Lotan and Critchfield 1990; Langdon, Pauchard, and Aguayo 2010).

4.1.2. Tree-ring width chronologies comparison

Analyzing the raw chronologies illustrated in graph 3, tree-ring width trends show a growth peak during the juvenile phase, lasting roughly for the first two decades of trees' life, followed by a steady decrease with the age. This trend can be explained as a normal age-related trees' response to the environment. Young trees often go through a period of juvenile growth during which they produce larger than average growth rings (Speer 2010). Alongside physiological growth patterns, this higher growth is also explained by the effect of the great resources availability that leads to low competition between seedlings and saplings. This phase lasted until the complete crown coverage, which caused an increase in the competition and a subsequent stabilization of growth. This is visible in all sites' chronologies (graphs 3), mainly due to the even aged structure that characterizes each plantation.

Standardized tree ring chronologies illustrated in graph 2 allowed the analysis of pointer years characterizing each site's growth patterns. Negative peaks are in common in all Iceland sites (see in particular 2011 and 2015, graphs 2A-D), and this can be related to cold spells during the growing season, which are often widespread all across the island, due to its characteristic position in the Atlantic Ocean and the strong climatic effects of the Icelandic Low (a semi-permanent center of low atmospheric pressure between Iceland and southern Greenland) (Einarsson 1984; Hanna, Jónsson, and Box 2004). Moreover, the northern provenances of seed could explain an intrinsic sensitivity to spring frost, as reported in a study on cold adaptation of coniferous species by Montwé et al. (2018). Nevertheless, during core samples analysis, this issue seemed not that relevant, as frost rings have been detected only in a few samples. In this way, this could be considered the positive result of the long trials made by IFS on seed provenance which lead to the selection of the best ecotypes for Iceland climate (Blondal 1987; Eysteinsson 2017).

Moreover, going in detail on Norway spruce, its chronologies show high fluctuation, beginning in the 90s both in Italian and Icelandic sites. This pattern is probably related to climate, hypothesis confirmed also by Stopar et al. (2018) in a study on the radial growth of Norway spruce in natural and secondary stands in Slovenia. In fact, their analysis of pointer years suggested that extreme events (exceptionally warm and dry years) are quite common and widespread in the last 30 years. Sangermano (2012) in his study (which analyzes 34 cores samples included also in the present thesis) has reported the same fluctuations (with apexes in 1989 and 2008) regarding Norway spruce in the Apennines (especially site FABPA). According to Sangermano (2012) this pattern can be considered once again as of climatic origin, given the intensification of years with hot and dry summers in the last decades. Moreover, as previously reported, Norway spruce's location far outside its optimal range, especially concerning Icelandic sites, could further influence the species sensitivity to local and global climate fluctuations.

The side species analyzed in this thesis, Sitka spruce (Site R1) and lodgepole pine (Site S2), show similar growth trends, even though they appear to be less influenced by climate variability, as also proved by their chronologies' statistics, likely thanks to their broader ecological amplitude (Lotan and Critchfield 1990; Langdon, Pauchard, and Aguayo 2010; Houston Durrant et al. 2016). However, the Sitka spruce chronology shows some anomalies in the pointer years, sometimes in contrast with the common trend emerged from Icelandic sites. The explanation is probably related to the major outbreaks of green spruce aphid occurred in the last decades (*Elatobium abietinum* (Walker), Aphididae), which have been accidentally introduced in Iceland in the late 1950s (G. Halldórsson et al. 2003). The insect attacks spruces, especially North American species, causing heavy defoliation, but rarely killing trees (G. Halldórsson et al. 2003). Anomalous negative pointer years in Sitka spruce chronologies, i.e. 2004 (Graph 3A) can therefore be explained as a result of this pest.

4.2. Climate-growth relationships

As previously reported in the results chapter (3.3, graphs 4 and 5), the climate influence on growth changes according to latitude: in Iceland, it is mainly associated to temperature whereas in Italy it relies mainly on precipitation. Focusing on Icelandic sites, temperature influence on growth is concentrated in a 4-month period from May to August. Norway spruce has shown a positive correlation especially with June, July and August temperatures and a negative correlation with April temperatures. A similar summer response has also been showed by Andreassen et al. (2006) in a study on the regional differences in climatic responses of Norway spruce in Norway, where, in northern regions and at high altitudes, June temperatures mainly influenced the growth. However, another study by Liepe et al. (2016) in similar latitudes in western Canada, suggests for a similar species (*Picea glauca, P. Engelmannii*, and their hybrids) how adaptation to climate does not always linearly correspond to temperature gradients. This said, the peculiarity of Iceland climate, given also the continental attitude of Norway spruce, could

strongly influence and modify the species performance causing anomalies to the typical behavior of the species (Caudullo, Tinner, and Rigo 2016). This could partially explain the negative correlation with April temperatures. Unfortunately, there is a lack of studies assessing the complex climate-growth relationships of Norway spruce in Iceland, mostly given the relative low relevance of Norway spruce in Iceland context (Snorrason and Kjartansson 2017). Sitka spruce and lodgepole pine climate-growth relationships confirmed the same type of association with summer temperatures, even though they present overall lower correlation values. Regarding Sitka spruce, it is also important to consider the relationship with precipitation, especially in the five-month period of the previous year (June to October, graph 5), which suggests an ambivalent response of growth to climate. In particular, within this five-months window, the species shows a negative correlation with temperature and a positive correlation with precipitation, according to its intrinsic oceanic attitude (Houston Durrant et al. 2016). However, as previously reported, another reason for the anomalies in the correlation profile could be related to green spruce aphid outbreaks (G. Halldórsson et al. 2003), which can strongly influence the growth, altering the correlation profile with climate.

Moving to Italy, especially for FABPA (graphs 4 and 5), the results suggest that Norway spruce growth relies more on precipitation than temperature, which on the opposite negatively influences the species' growth, both in previous and current year summer. A similar growth pattern has been reported also in the thesis by Sangermano (2012). In particular, the correlations profile with monthly rainfall shows that radial growth is favored as summer (July in particular) rainfall increases (FABPA, graph 6). This behavior is in line with the species' ecological needs, which requires high water supplies and is very susceptible to drought (Sangermano 2012; Caudullo, Tinner, and Rigo 2016). There are also some significant correlation summer temperatures. The months that have a significant negative effect are especially July of the current year and June of the previous years for site FAPBA. High temperatures in these months therefore result in reduced tree ring width (Sangermano 2012). However, there are some divergences with Sangermano's results, especially in the number of significant months, which are more compared with the results reported in this thesis. This characteristic growth profile has been previously reported also in studies conducted in Southern Alps, a location close to the southern limits of the species distribution. For example, Di Pierro et al. (2016) have suggested that precipitation appears as the most important environmental variable associated with the high sensitivity of Norway spruce to soil water supply. Significant correlation between tree-ring width and spring precipitation was also observed by Čermák et al. (2017) for the period 1964–2012. A similar response has been reported by Rybníček et al. (2010).

The analysis of the supporting species, Sitka spruce and lodgepole pine, corroborated the results, highlighting the relevance of summer temperature for the species beyond the northern limit of their distribution, with a partial effect of previous growing season. These biogeographic patterns have been previously showed by Babst et al. (2013), who evaluated the climate sensitivity of model-based forest productivity using a continental-scale tree-ring network between Europe and North Africa (30-70°N,

10°W-40°E). The model showed that temperature controls dominate forest productivity at high-elevation and high-latitude areas whereas moisture sensitive sites are widespread at low elevation in central and southern Europe (Babst et al. 2013). Moreover, the study highlighted that carry-over effects from the previous growing season can significantly influence tree growth.

4.3. Shift in distribution ranges: projections and challenges

In the last decades forest ecosystems are globally experiencing some of the most rapid, clear and significant changes related to global warming (IPCC 2014). As reported in the introduction of this thesis, projections made in the last years suggest by 2100 a temperature increase between 2-3 °C to 4–5 °C in the European Continent, though with some regional variability (Lindner et al. 2010). Plotting the available

climate data collected for this thesis, the warming trend is clearly visible in graph 7 (A-B): mean temperature measured for a 64-years period for Iceland and 138-years for Italy showed an increase of 1.5 and 2 °C respectively. Regarding precipitation, the trend is not so evident (graph 8), even though the records reveal a higher inter-annual variability, similar to IPCC (2014) projections regarding changing patterns in climate events (e.g. of extreme meteorological intensification events) and as showed by standard deviation values (see paragraph 4.1). In such climate scenario several studies tried to understand how forest growth pattern and the migration ability of trees would be affected. As Aitken et al. (2008) have suggested, trees will need to move more than 1000 m per year to keep pace with the climate to which they are optimally adapted. On the other hand, a study of five tree species in the eastern United States has showed very low probabilities of natural dispersal beyond 10-20 km from current species boundaries by 2100 (an average of 100-200 m per year) (Iverson, Schwartz, and Prasad 2004). In a study on projected migration requirements for 24 western North American tree species by Roberts and



and for Italy (B).

Graph 8 (below). Total annual precipitation trend for Iceland (A) and for Italy.

The curves have been developed averaging the available climate data collected for the climate growth relationships analysis. The reported observation periods are 1955-2019 for Iceland and 1880-2018 for Italy.

Hamann (2016), results have demonstrated that speeds to reach the nearest future climate refugia still exceed the fastest reconstructed post-glacial migration rates, while suggesting that qualitatively different migration patterns may emerge in the future due to landscape complexity.

The boreal area, will be the most affected by climate warming (Kaplan and New 2006; MacDonald, Kremenetski, and Beilman 2008; Soja et al. 2007; IPCC 2014). This area is currently covered by ice sheets and biomes such as tundra and taiga that could experience major changes in species and habitat distribution over the future (MacDonald, Kremenetski, and Beilman 2008). As suggested by Taggart and Cross (2009), if global warming causes a significant vegetation redistribution, northern latitudes biomes might experience a northward migration of boreal forest characterized by loss of taxa and extensive community reorganization. As individual taxa are pushed to their limits, rates of migration and biotic stress will eventually result in pest outbreaks and diseases, resulting in the dominance of high arctic lowlands by low diversity larch-dominated forest, with evergreen taxa restricted to mountain refugia (Taggart and Cross 2009). Lindner et al. (2010) have reported the same outcome, expanding the predictions of important potential impacts of climate change on forests for Temperate Oceanic, Temperate Continental, Mediterranean, and mountainous regions. Especially in northern and western Europe, the increasing atmospheric CO₂ concentration and warmer temperatures are expected to improve forest growth and wood production, while increasing drought and disturbance risks will cause adverse effects. These negative impacts are likely to outweigh positive trends in southern and eastern Europe, especially in the Mediterranean regions, where productivity is expected to decline due to increased droughts and fire risks. (Lindner et al. 2010). This highlights once again the relevance of temperature for tree growth within the northern latitudes and of precipitation towards south as emerged in the results (chapter 3.3) of this thesis and reported by Babst et al. (2013).

4.4 Limitations of the study

The main limitation for the study resides in the limited length of the tree-ring records. In fact, the period of 52 years used for building climate-growth relationships, is rather short for a sound statistical comparison. Unfortunately, this window was the maximum available for this thesis, especially due to the shortness/lack of climate data and the age of the plantations, dating back to maximum 1948, in Iceland (Rauðavtn plantation, site R1). Moreover, the number of core samples has not always been adequate. This is the case for site S2, with14 samples and especially for site TREPA, with 11 samples, which showed very low correlation with almost all climate variables. During cross-dating, in fact, this sample size could fail in providing a strong statistical evaluation and therefore could cause biases in the climate-growth correlation profile. Moreover, the complete measurements of height and DBH, available instead only for site R1, H3 and V4, could have provided a more thorough analysis of trees growth. The lack of these data is due to limited time and resources.

The search for similar studies has been difficult, showing a general shortage of investigations dealing with trees' (mainly Norway spruce) behaviors and growth patterns beyond the limit of the species'

distribution, especially considering both northern and southern limit at the same time. Many studies are based on models and focus on forests and ecosystems migration projections. Moreover, I found a lack of studies concerning Norway spruce in Iceland and in central Italy. This made the present work more complex. This is probably due to the scarce importance and presence of this species in these areas, respect the more productive and climatic-adapted taxa (e.g. Siberian larch and Sitka spruce in Iceland; silver fir and beech in Central Italy).

Finally, the results showed in this study regarding the Icelandic part, must also be considered in the light of the particular climate of the island. The high variability of temperature and precipitations, its peculiar position in the Atlantic Ocean and the phenomenon of the Icelandic Low could strongly influence treegrowth patterns, and results in a more complex and unpredictable association pattern.

5. CONCLUSION

The aim of this thesis was to study, using dendrochronological techniques, the growth response to climate of Norway spruce beyond its natural distribution. The analyzed sites, all composed by artificial plantations, were chosen to be representative for the growth of Norway spruce beyond its distribution range. In particular, Iceland plantations allowed the study of growth patterns north of the distribution limit of the species, while the central Italian Apennines stands were chosen to study the growth beyond the southern limit.

The analysis of pointer years and of radial increment of trees showed an overall high fluctuation in the tree-ring width, beginning in the 1990s both in Italian and Icelandic sites. This pattern is probably related to climate, testifying an increase in the years with hot and dry summers in the three decades. Moreover, the climate-growth correlation profiles highlighted a differentiation in the action of climate on tree growth, which seems to vary according to latitude: at northern latitudes, within the Icelandic sites, Norway spruce growth is mainly affected by temperatures, especially mean summer temperature (June July and August), whereas, towards the southern latitudes, within the Italian sites, precipitation regime plays a major role, especially during July of the current year and June of the previous year. In Italy, the TREPA site showed an overall low correlation with climate variables, probably due to the amount of data, too short to build strong correlations. The inclusion of Sitka spruce and lodgepole pine climate-growth relationships proved useful to better understand growth patterns in Iceland, supporting the growth trend showed by Norway spruce.

Considering the present warming scenario and the general uncertainties on tree migration and growth patterns, the results of this thesis can add a contribution on a better understanding of the growth of species located outside their distribution and therefore on how trees might behave in the future. Building a strong database on tree growth patterns in these areas through similar studies could allow a more accurate understanding of species responses under different climate scenarios. This could lead to stronger predictions on plants' range expansions or contractions, changes in growth patterns, changes in productivity, and other cascading responses. Moreover, the results can be useful in further developing strategies such as assisted migration: knowing the future trees requirements can facilitate the movement of species to improve natural population dynamics and range expansion with the purpose of ensuring forest plantations resistance within future climates. Therefore, well-planned translocations of species may reduce the risk of extinction, as well as increase the number of potential taxa creating new assemblages in a fluid landscape responding to the major climate changes the world will experience. The analyzed plantations, especially in Iceland, proved the efficacy of such approach: trees seem to be responding positively to Icelandic climate regime, showing good growth values and overall good health conditions. This opens the way to two important opportunities: ensuring the expansion of species in areas hardly reachable through natural migration and employing pristine lands to establish forests, one of the main tools in the fight against climate change.

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APPENDIX

In table 3 it is possible to see the height and dbh measurements for each tree. Even though the available data regards only three sites out of six (R1, H3 and V4), all located in Iceland, this information is still relevant, being them an additional tool for describing and better understand growth patterns.

R1			H3			V4		
Sample	dbh (cm)	H (m)	Sample	dbh (cm)	H (m)	Sample	dbh (cm)	H (m)
1	28.3	21.7	1	24.6	13	1	19.8	11.2
2	39.8	17.4	2	21.3	12.8	2	16.5	11.9
3	34.1	15.8	3	38	18.8	4	18.5	12.5
4	30.9	19.5	4	38	19.2	5	17.2	13
5	26.4	18.4	5	34.3	18.1	6	20	11.7
6	30.2	16.8	6	34.2	14	7	22.4	12.5
7	24.8	16	7	31.5	16.3	8	18.2	10.3
8	29.9	17.5	8	35	18.5	9	18.8	10.7
9	29.3	18.2	9	15	12.1	10	17.8	9.9
10	28.6	17.2	10	17.2	12.7	11	17.9	12.2
11	33.7	18.2	11	21.1	12.2	12	15.1	10.7
12	43.0	17.2	12	19.1	12.4	13	12.5	9.7
13	36.6	18	13	14.5	11.1	14	15.2	9.7
14	31.8	18.2	14	20	12.3	15	17	10.6
15	22.9	13.8	1T	21.4	13.2	16	19.8	10
16	15.3	14	2T	18.4	12.2	17	18.9	9.6
17	14.3	14.5	3T	21.3	14.2	18	13.9	10.1
18	15.6	15.2	4T	17.5	12.3	19	12.4	9.6
			5T	18.6	14.7	20	16	10.4
			6T	20.2	14.8	21	16	10.2
			7T	16.2	11.2	22	9.6	15.2
			8T	19.9	11.9	23	7.9	12.2
			9T	22.4	15.1			
			10T	22.6	14.6			

The regression analysis performed to explain the relationship occurring between dbh and H, has

Table 3. Measurement of height (H) and diameter at breast height (dbh) for each tree within sites R1, H3 and V4. Letter T in the Sample column stands for "thinned", indicating a tree sampled in a thinned area of the forest.

been computed using all the measurements reported in tab 3, hence including both Sitka spruce and Norway spruce. As visible in graph 7, the analysis showed a coefficient of determination R^2 of 0.6077, not particularly high, partially due to the limited amount of the data and the presence of sampled trees coming from thinned forests, condition that could modify the dbh- H relationship in respect of forests where thinning has not been performed. In table 4 the results of the regression analysis are reported. P-value is a number smaller than 0.00001, therefore it is possible to assume p < 0.001.

	Coefficients	Standard Error	t Stat	P-value	Lower 95%
Intercept	6.899543492	0.74611772	9.247258581	7.05192E-12	5.395842031
X Variable (dbh)	0.286046335	0.035235424	8.118146542	2.73E-10	0.215034004

Table 4. Coefficients and significance level for H-dbh regression analysis.





• R1 - Sitka spruce 📮 H3 - Norway spruce 🔺 V4 - Norway spruce